Season affects strength and direction of the interactive impacts of ocean warming and biotic stress in a coastal seaweed ecosystem

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Abstract

The plea for using more "realistic," community-level, investigations to assess the ecological impacts of global change has recently intensified. Such experiments are typically more complex, longer, more expensive, and harder to interpret than simple organism-level benchtop experiments. Are they worth the extra effort? Using outdoor mesocosms, we investigated the effects of ocean warming (OW) and acidification (OA), their combination (OAW), and their natural fluctuations on coastal communities of the western Baltic Sea during all four seasons. These communities are dominated by the perennial and canopy-forming macrophyte *Fucus vesiculosus*—an important ecosystem engineer Baltic-wide. We, additionally, assessed the direct response of organisms to temperature and pH in benchtop experiments, and examined how well organism-level responses can predict community-level responses to the dominant driver, OW. OW affected the mesocosm communities substantially stronger than acidification. OW provoked structural and functional shifts in the community that differed in strength and direction among seasons. The organism-level response to OW matched well the community-level response of a given species only under warm and cold thermal stress, that is, in summer and winter. In other seasons, shifts in biotic interactions masked the direct OW effects. The combination of direct OW effects and OW-driven shifts of biotic interactions is likely to jeopardize the future of the habitat-forming macroalga *F. vesiculosus* in the Baltic Sea. Furthermore, we conclude that seasonal mesocosm experiments are essential for our understanding of global change impact because they take into account the important fluctuations of abiotic and biotic pressures.

The global ocean has been taking up excess atmospheric heat and CO_2 and, owing to inertia within the energy and climate system, it is likely to do so for many years to come even if stringent greenhouse gas mitigation strategies were implemented today (IPCC 2014). Over the past decades, biological consequences of the resulting ocean warming (OW) and acidification (OA) have become increasingly visible in the natural environment (e.g., Harley et al. 2006; Laffoley and Baxter 2018) and a large amount of experimental data have facilitated estimates of future impacts on marine organisms under increasing levels of both factors (e.g., Kroeker et al. 2013). Yet, there still remains a substantial uncertainty about how direct impacts on single organisms, as assessed in "mechanistic approaches" (single species, single driver, microcosms; Boyd et al. 2018), are modulated in a community context by (shifting) biotic interactions (indirect impacts), and how they, cumulatively, lead to changes in structure and function of communities and ecosystems (e.g., Harley et al. 2017). To overcome this gap of knowledge, the scientific community has been aiming for more realism in ecological climate change research by means of upscaling experimental approaches in space (size of experimental unit), time (duration of experiment), and complexity (number of interacting species, number of drivers, number of generations, inclusion of natural fluctuations; e.g., Riebesell and Gattuso 2015; Wahl et al. 2016). Ideally, such mesocosm studies include two or more relevant global change factors (warming, acidification,

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pollution, deoxygenation; e.g., Doney et al. 2012) as well as their natural fluctuations at different temporal scales (e.g., from a few days of heat wave or upwelling, to seasons (Godbold and Solan 2013; Wahl et al. 2016). Incorporating several trophic levels (Blake and Duffy 2012; Best et al. 2015; Goldenberg et al. 2017), different ontogenetic stages (Byrne 2012; Byrne and Przeslawski 2013; Foo and Byrne 2017; Pansch and Hiebenthal 2019), populations (Saada et al. 2016), and generations (Kelly et al. 2011) further improves the ecological realism of these experimental approaches.

However, while along the gradient from tightly controlled and simple to complex and "natural" experiments, we gain ecological relevance but we lose precision (Carpenter 1996; Sommer 2012). The complementarity of both approaches seems therefore important, as scaling is a naturally bidirectional and iterative component of problem solving in ecology and in climate science (Osmond et al. 2004; Boyd et al. 2018).

By now, significant progress toward more realistic assessments has been achieved in multifactorial (several drivers) and multivariate (several responses) long-term mesocosm studies (Sommer 2012; Jokiel et al. 2014; Nagelkerken and Connell 2015; Riebesell and Gattuso 2015; Boyd et al. 2018). Several studies show the capacity of biotic interactions—or the shift of such—to modulate or even mask the direct impact at the organism level of global-change-driven abiotic environmental pressures, for instance, for parasite-host interactions (e.g., Kirk et al. 2018), pathogen-host interaction (e.g., Kiesecker and Blaustein 1995; Campbell et al. 2012), epibiont-host interaction (e.g., Werner et al. 2016*a*; Takolander et al. 2017), competition, and predation (e.g., Alsterberg et al. 2013; Falkenberg et al. 2013; Goldenberg et al. 2017; Provost et al. 2017). The amplification or buffering of environmental impacts by biotic interactions should be particularly pronounced where foundational, that is, habitat-forming, species are involved (Doney et al. 2012). Habitat forming macroalgae, for instance, at small spatial scales may act as community "rescuers" (Bulleri et al. 2018) by countering the effects of global change factors such as warming (e.g., Silliman et al. 2011), deoxygenation (e.g., Hiddink et al. 2015), acidification (e.g., Hurd 2015; Wahl et al. 2018), or eutrophication (e.g., Holmer et al. 2016). In consequence, a collapse of habitat-formers in response to environmental shifts may have severe ramifications to the entire community (Smale and Wernberg 2013; Bulleri et al. 2018).

In the present study, we compare the community level impacts of naturally fluctuating OA and/or OW, among different seasons of the year and with regard to their (mainly OW) direct effect at the organism level. Future high CO_2 conditions may enhance bottom-up control and competition by increasing photosynthetic rates in some algal groups (e.g., Kroeker et al. 2010; Hepburn et al. 2011 and references therein, Alsterberg et al. 2013; Goldenberg et al. 2017). Additionally, changes in seawater pH and carbonate chemistry are expected to, mainly adversely, affect shell-production and growth in calcifying organisms (Michaelidis et al. 2005; Gazeau et al.

2007; Wood et al. 2008), which at the community or ecosystem level may alter species composition and nutrient cycling.

OW according to the metabolic theory of ecology (e.g., Brown et al. 2004) is expected to affect several hierarchical levels of biological organization, from energy uptake rates through population dynamics and species interaction to community structure and functioning (Schramski et al. 2015). Typically, physiological performance rates (e.g., photosynthesis, respiration, growth, and ingestion) increase gradually with warming from a critical thermal minimum (CT_{min}), reach maximum rates at an optimal temperature (T_{opt}), then decrease more rapidly when temperature increases toward the critical thermal maximum (CT_{max}) (e.g., Angilletta 2006; Sinclair et al. 2016, see also Fig. 1). When within the same system (organism, community) contrasting processes like photosyntheis (O_2 production, inorganic C consumption) and respiration (O_2 consumption, inorganic C production) simultaneously respond to warming, it may be useful to consider their combined response, for example, metabolic balance (Duarte and Regaudie-De-Gioux 2009). Thermal performance curves (TPCs) which express the impact of a specific temperature (range) on organisms may differ conspicuously among entities such as species, populations, genotypes, life stages, and response traits (e.g., Pörtner and Farrell 2008; Byrne et al. 2010; Kingsolver et al. 2011; Sinclair et al. 2016; Foo and Byrne 2017). Furthermore, temperature and its impact on organismal performance may vary at small scales (< 1 m) depending on microhabitat characteristics (e.g., Lima and Wethey 2009; Tait and Schiel 2013) in addition to the better studied large-scale (latitudinal) variation, which may (Pearson et al. 2009) or may not (Wernberg et al.
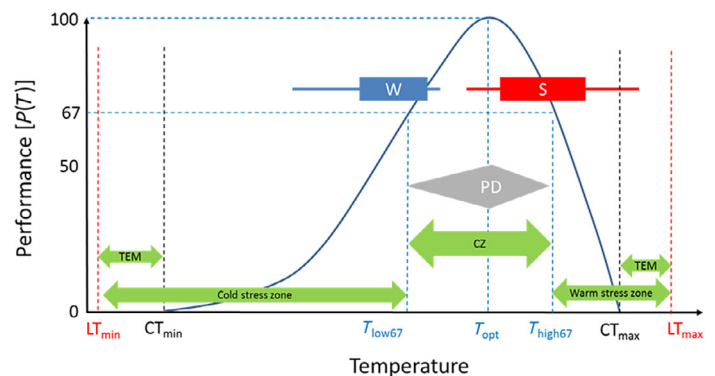
Fig. 1. Idealized TPC (modified after Woodin et al. 2013 and Sinclair et al. 2016) indicating the various critical temperatures, which were used to define different intensities of stress (see text). The performance diamond PD depicts the increase of performance from low (but not zero as the symbol suggests) at T_{low67} to maximal at T_{opt} to low (but not zero as the symbol suggests) at T_{high67}. Cold resp. warm stress zones are the temperature ranges between the lower lethal temperature and the cold end of the comfort zone and the higher lethal temperature and the warm end of the comfort zone. The transient event margins are the cold and warm temperature ranges the organism in question can only tolerate transiently. The horizontal box-and-whiskers symbols are examples how fluctuating winter and summer temperatures may produce different intensities of stress (at different frequencies).

2016) affect the shape of the thermal response of populations of the same species (expressing or not local adaptations).

It is tempting to infer the ecological or evolutionary fate of a species subject to OW from its thermal tolerance range (e.g., Somero 2011; Vasseur et al. 2014) as assessed in the absence of other abiotic or biotic drivers. In addition, inference of thermal tolerances from distribution patterns or transplantation experiments is common (Hijmans and Graham 2006; Elith and Leathwick 2009; Peterson et al. 2019). However, at any given temperature, interacting organisms belonging to the same or different species will be found at different distance from their specific T_{opt} and, consequently, at different levels of their specific performance. Relative performance levels determine the interaction strengths (and sometimes even the direction of interaction effects) among competitors, consumers and their prey, parasites and their hosts, and so on (e.g., Dell et al. 2014; Gilbert et al. 2014; Provost et al. 2017). Thus, any temperature change may shift the strength and/or quality of biological interactions and, thus, modulate the direct effect of temperature on performance, species abundance and, ultimately, community composition and functioning.

In order to explore the congruency (or lack thereof) between direct global change impacts at the organismal level, and the organism response in the community context (in different seasons), we investigated the effects of ocean acidification, warming, and their combination (OA, OW, OAW) on different organizational and functional levels (performance traits, species, community, functional groups) of a benthic community in the western Baltic Sea combining benchtop and mesocosm approaches. In a series of medium-term mesocosm experiments (2.5–3 months duration each), we assessed community level impacts across all four seasons. As the mesocosm experiments were operated in a flow-through mode, the natural fluctuations in light, nutrients, temperature, salinity, O_2, and CO_2 at all temporal scales (hours to months) were incorporated (Wahl et al. 2015*a*).

Since in the course of the mesocosm experiments, we identified OW—relative to OA—as the clearly dominant global change driver (Mensch et al. 2016; Werner et al. 2016*b*; Raddatz et al. 2017), the single-species experiments (benchtop) focused mainly on thermal performances (e.g., Woodin et al. 2013). Finally, we compared the individual species-based predictions to the results obtained in the described four seasonal community mesocosm experiments for an estimation of biotic modulation of OW effects.

The study system as a "whole" (ecological community) or "parts" (single-species, single drivers [following Odum 1984]) comprised the brown macrophyte *Fucus vesiculosus* and its associated micro- (colonial diatoms, bacteria) and filamentous macro-epiphytes (e.g., *Ulva* spp., *Cladophora* spp., *Pilayella* spp.), their predominant crustacean (*Gammarus salinus*, *G. oceanicus*, *G. locusta*, *Idotea balthica*, *I. chelipes*) and gastropod (*Littorina littorea*) mesograzers, calcifying filter feeders (the crustacean *Amphibalanus improvisus* and the mollusk *Mytilus edulis*), and a predatory seastar (*Asterias rubens*). The selected species represent the main players of the natural shallow hard bottom benthic community of the SW-Baltic Sea—except fishes. In this ecosystem, *F. vesiculosus* (hereafter *Fucus*) is one of the most dominant perennial and canopy-forming macrophytes in the rocky inter- and shallow subtidal zone (Kautsky et al. 1992) and functions as an ecosystem engineer providing biogenic structure, food, shelter, and nursery ground to a diverse associated community (e.g., Kraufvelin and Salovius 2004). The *Fucus* system as a whole functions as key nutrient sink and carbon storage of the coastal zone (Kawamitsu and Boyer 1999; Bokn et al. 2002). Its ecological importance, however, ranges well beyond its coastal habitat boundaries as its primary (and secondary) production is exported as floating algae (Rothausler et al. 2015) or detritus (Krumhansl and Scheibling 2012). The *Fucus* system is maintained by fine-tuned biotic interactions such as competition for resources like light, nutrients and space (*Fucus* vs. epiphytes, *Fucus* vs. filter feeders), consumption, and mutualistic co-occurrence (e.g., competitive epiphytes control by mesograzers; Korpinen et al. 2007; Jormalainen et al. 2008). It can be assumed that beneficial or harmful effects of environmental change on any of these key components of the *Fucus* system modify their intra- and interspecific interactions potentially resulting in an alternation of the system's composition and functioning, and services. Already today, *Fucus* communities as many other macroalgal assemblages worldwide are under substantial pressure (Wahl et al. 2011, 2015*b*).

In light of the above, the mesocosm experiments were designed to investigate single and combined effects of OW and OA on (1) the abundance and biomass of selected species in the *Fucus* community, and/or (2) physiological responses of the key taxa with regard to photosynthesis, storage products, feeding, growth, reproduction, metabolic rate, as well as to investigate (3) the seasonal variability of these effects and (4) the resulting community restructuring. The mechanistic single-species experiments elucidated the relationships between temperature, OA (for selected cases), and the same or similar performance traits but in the absence of biotic interactions.

Our main research questions, thus, were the following:

1. How do OW and/or OA impact a Baltic macrophyte community at the levels of species performances, population dynamics, or community structure?
2. How do these impacts vary with season?
3. How are selected performance traits affected by temperature in the absence of biotic interactions?
4. How well can modeled TPCs based on individual species experiments predict the response of species to OW in a near-natural community context?

Materials and methods

Seasonal mesocosm community experiments

The seasonal mesocosm experiments were performed in the Kiel Outdoor Benthocosm (KOB) infrastructure at GEOMAR

Kiel, Germany, between 2013 and 2014. The KOB consists of 12 tanks (experimental units) with insulated walls containing ca. 1500 L volume and are situated on a floating platform in Kiel Fjord. The tanks constitute fully independent experimental units in all regards and work in a flow-through mode with unfiltered fjord water, passing through the tanks with a rate of ca. 1 tank volume per 24 h. Thus, all natural fluctuations of environmental factors (e.g., salinity, temperature, oxygen, nutrients, plankton) with frequencies from hours to seasons were allowed in the tanks. Treatment levels (e.g., warming, acidification) were added or subtracted in real time to the actual in situ levels by an independent and fully computer-controlled assemblage of sensors, heaters, chillers, and CO_2 pumps per experimental unit. The full technical details of the KOB facility, the experimental setup, and monitoring are described in Wahl et al. (2015*a*). Abiotic environmental data of the experiments can be found at http://doi.pangaea.de/10.1594/PANGAEA.842739. Two temperature and CO_2 levels (ambient vs. elevated) were full-factorially crossed in all experiments. Treatments were (1) the ambient (fluctuating) in situ Kiel Fjord conditions, (2) incremental warming by 5°C (OW), (3) CO_2 enrichment (of the head space) by ca. 600 μatm (OA), and (4) a combination of both (OAW). These manipulations were based on Baltic Sea climate change predictions for 2100 (BACC Author Team 2008, 2015; Schernewski et al. 2011). All treatment combinations were replicated three times. Four seasonal experiments were conducted in spring (04 April 2013–19 June 2013), summer (04 July 2013–17 September 2013), autumn (10 October 2013–17 December 2013), and winter (16 January 2014–01 April 2014). Running separate seasonal experiments ignored potential carry-over effects but allowed us to assess seasonal differences in the magnitude and direction of the impacts. In the onset of each experiment, complete *Fucus* communities which included the habitat-forming macrophyte, its associated epiphytes and mesograzers (the isopod *Idotea* spp., the amphipod *Gammarus* spp.), the gastropods *L. littorea*, filter feeders (*M. edulis* and *A. improvisus*), and their predator starfish *A. rubens* were collected from the field and placed in the KOB. Care was taken to match the identity, abundance, and biomass of all components with in situ conditions in the respective season and among all tanks (details in Graiff et al. 2015*a*; Werner et al. 2016*a,b*). While adult *Idotea* sp. could generally be identified to the species level (*I. balthica*, *I. chelipes*), this was impossible for the juvenile isopods and only possible after dissection for the gammarids. For these reasons and because of wide ecological overlap (e.g., Hällfors et al. 1981; Leidenberger et al. 2012), we lumped these species into two functional groups: "*Idotea* spp." and "*Gammarus* spp." *I. balthica* generally constituted > 80% of the isopods. Dominance in the gammarids tended to shift from *G. salinus* and *G. oceanicus* in the colder months to *G. locusta* in the warmer season. Hence, all experimental communities started with composition and densities being almost identical to each other and to the respective natural *Fucus*

communities of the western Baltic Sea. The experimental communities were gradually acclimatized to the target treatment values by slowly increasing temperature and pCO_2 levels over 1 week. During the experiment, additional species such as the snails, *Rissoa* spp. and *Hydrobia* spp., recruited to the tanks. All abiotic variables assessed in the KOB experiments are available at http://doi.pangaea.de/10.1594/PANGAEA.842739. Per seasonal study, a wide variety of response variables (Table 1) were sampled at various temporal intervals (for details, see Werner and Matthiessen 2013; Graiff et al. 2015*a,b*; Al-Janabi et al. 2016*a,b*; Werner et al. 2016*a,b*; Graiff et al. 2017; Raddatz et al. 2017). The results were published in the cited references with the raw data being accessible on Pangaea (DOIs in the cited articles). In this synthesis, the final sampling data points in each season (i.e., after approximately 3 months of incubation) and for all treatments (http://doi.pangaea.de/10.1594/PANGAEA.842739) were included for the following responses in the *Fucus* system: *Fucus* performance (composed of the traits listed below), overgrowth by epiphytes, grazer abundance, filter-feeder growth, and sea star survival. Gross primary production (GPP as μmol O$_2$ [g FW]$^{-1}$ h^{-1}, FW denotes fresh weight) of *Fucus* was assessed as the change in O_2 concentration (using oxygen optodes and planar SP-PSt3-PSUP-YOP-D5 oxygen sensor spots from PreSens GmbH, Regensburg, Germany) during an incubation of 2 cm long vegetative apical tips in closed 25 mL chambers in the dark for 30 min (respiration, R) and subsequently exposed to light (200 μmol m^{-2} s^{-1}; 150 W halogen lamps, HLX 64634, OSRAM GmbH, Bad Homburg, Germany) for 10 min (net primary production [NPP]). The accumulation of the storage product mannitol (mg [g DW]$^{-1}$) dry weight was analyzed by (HPLC) High-Performance Liquid Chromatography in the extracts from freeze-dried vegetative apices of *Fucus* following the method of Karsten et al. (1991). The investment into reproduction (measured as the mean proportional biomass of fertile thallus tips relative to sterile thallus tips was assessed regularly during and once at the end of each seasonal experiment (details in Graiff et al. 2017). Defenses against microbial fouling were quantified by sampling 10 nonfertile and unfouled apical tips of *Fucus* of ca. 10 cm length, spin-drying them for 20 s and dip-extracting them for 4 s in a 1:1 mixture of methanol and hexane. This extract was coated at near-natural concentration (i.e., as found on the thallus surface) on the inner wall of the wells in a 96-well plate and subsequently exposed for 3 h to colonization by bacterial strains isolated from the *Fucus* habitat. After thorough rinsing of the wells followed by a staining with SYTO® 9 Green Fluorescent 267 Nucleic Acid Stain (Life Technologies), settled bacteria were quantified using a plate reader (Hidex Chameleon IV, Turku, 271 Finland, more details in Raddatz et al. 2017). Defenses against macrofouling (e.g., barnacles, mussels, algae) were assessed by coating gel-substrata with natural concentration of the *Fucus* surface extract and exposing them to natural fouling in Kiel fjord for 6 d (details in Raddatz et al. 2017). Defenses against grazing were assessed by incorporating freeze-dried *Fucus* (sampled at the end of each seasonal experiment) at

Table 1. Effects of OW as extrapolated from the organismal (top, benchtop) responses and as found at the community (bottom, KOBs) level. The first is expressed as the increase or decrease of degree-days the organisms spent outside the modeled comfort zone in the KOB relative to the ambient temperature regime. The second are the effect sizes of warming effect in the KOB expressed as positive or negative additive inverse (opposite) Hedges' *g*. Reddish hues indicate stress intensification by OW and greenish hues indicate stress relaxation by OW. Colors saturation relates to effect strength.

Benchtop responses	Modeled responses to OW (degree-days outside comfort zone)			
	Spring	Summer	Autumn	Winter
Fucus photosynthesis (NPP)[1]	−13	71	−2	−107
Fucus reproduction[2]	0	22	0	0
Fucus growth[1]	−71	202	−102	−294
Antigrazing defense[2]	−122	189	−203	−317
Anitfouling defense[1]	−20	81	−9	−152
Gammarus feeding[3]	−133	79	−223	−317
Idotea feeding[1]	−15	62	−3	−118
Littorina feeding[3]	−3	148	0	−46
Fouling[1]	−16	0	−4	−124
KOB responses	**Real responses to OW (inverse Hedges' *g*)**			
	Spring	Summer	Autumn	Winter
Fucus photosynthesis (NPP)	−0.04	3.84	0.1	0.07
Fucus reproduction	0.41	2.72	0.24	0.04
Fucus length growth	−0.13	2.27	−0.01	0.09
Antigrazing defense	−0.09	0.81	0.13	0.01
Antifouling defenses	−0.1	0.15	−0.03	0.11
Gammarus biomass	0.14	0.52	0.01	−0.68
Idotea biomass	−1.15	1.44	−0.56	−0.4
Littorina biomass	0.13	0.12	−0.23	−0.07
Fouling by macroepiphytes	−0.69	−0.7	−0.71	0.16

Best fitting model used: 1. Quadratic, 2. Gaussian, and 3. exponentially modified Gaussian.

natural concentration in agar, which subsequently was offered for 20 h as feed pellet together with a control pellet (*Fucus* from the fjord, two-way choice) to the regional important grazer *I. balthica*. The relative palatability was used as a measure for defense (details in Raddatz et al. 2017). *Fucus* performance also included growth rate, which was assessed as length increment of growing tips (gross growth) or biomass change (tissue production minus tissue lost to grazing, net growth) assessed repeatedly during each seasonal experiment and then averaged (details in Graiff et al. 2015*a*). The microfouling (mainly diatoms) under the different treatments was assessed as the dry weight of foulers settling during a seasonal experiment on ceramic tiles exposed among the *Fucus* individuals in each tank (Werner et al. 2016*a*). Macroepiphytes (mainly filamentous algae) were directly harvested form all the *Fucus* surface in a given tank at the end of each seasonal experiment, and expressed as dry weight per tank (details in Werner et al. 2016*a*). As a proxy for potential grazing pressure on epiphytes (and *Fucus*), we used the populations size (total biomass) of the relevant mesograzer taxon per tank by the end of each seasonal experiment (*Idotea* spp., *Gammarus* spp., and *L. littorea*, details in Werner and Matthiessen 2013; Werner et al. 2016*b*). The response of filter feeders to the

simulated climate change was assessed as the mean growth rates (*μ*m length d^{-1}) of the barnacle *A. improvisus* and the bivalve *M. edulis* during each seasonal experiment. The response of their main consumer, the sea star *A. rubens*, was expressed as survival rate by the end of each seasonal experiment.

Benchtop single-component experiments on temperature and pH dependency of processes and interactions

The summary of benchtop experimental conditions, including temperature levels, pCO$_2$ levels, duration, period, and acclimation time, is detailed in Supporting Information Table S1a.

Thermal responses

Fucus responses. In the various benchtop experiments, a range of (PAR) Photosynthetically active radiation levels (93–165 *μ*mol m^{-1} s^{-1}) was used attributable to the possibilities in the various laboratories. However, irradiation was always identical among treatment levels within single experiments and always was within the "comfort zone" of *F. vesiculosus* (i.e., < 67.5% of P_{max}, *see* Supporting Information Fig. S1a) with regard to O$_2$ production or consumption measured by microsensor measurements (Unisense, Aarhus, Dk) of O$_2$ concentrations

at the thallus surface of freshly collected *F. vesiculosus* exposed to PAR levels of 0, 10, 55, 190, 450, and 800 μmol m^{-2} s^{-1} (pH 8.2, salinity 18.6, temperature 19.5°C) (courtesy Marlene Wall, GEOMAR). The O_2 production was calculated from the gradient in the diffusive boundary layer following Lichtenberg et al. (2017). Only for the assessment of benthic microfouling an irradiation level of 60 μmol m^{-1} s^{-1} was used which corresponds more to the more shaded conditions among macroalgae (M. Wahl pers. obs.).

Fucus photosynthetic rate and respiration, metabolic balance. *Fucus* individuals were collected in the Kiel Fjord (54°38′N 10°20′E) and transported to the facilities of GEOMAR. They were placed in tanks inside a climate chamber at 15°C for 24 h with continuous water flow. The tanks were equipped with a combination of light sources providing a photon fluence rate of 165 μmol photons m^{-2} s^{-1} (eco+ LED-row SUN-SET 3500K 34W and eco+ LED-row DAY 5500K 34W, LEDAquaristik UG, Hövelhof, Germany). The algae (11.2 g FW, SD 5.5 g), after the removal of macroepiphytes, were kept under 12:12 h light:dark cycle, and after 24 h were transferred to buckets of 10 L volume (two individuals per unit) which were continuously aerated and kept in a flow-through mode (13 L d^{-1}) of sand-filtered fjord water. The buckets were placed in thermobaths controlling the treatment temperature. After an acclimation phase of 1 week, the water temperature was increased or decreased by 1°C d^{-1} with a staggered start day in order to reach the target temperatures of 5, 10, 15, 20, 22, or 25°C on the same day. Weekly, photosynthetic (NPP, under light) and respiration (in the dark) rates of *Fucus* were measured individually in 6-liter gas-tight chambers (at 165 μmol m^{-1} s^{-1} and in darkness, respectively) equipped with a stirrer and a noninvasive oxygen sensor spot PSt3 (PreSens Precision Sensing GmbH, Regensburg, Germany). The chambers were filled with seawater filtered through 1 μm polypropylene fiber filter. Oxygen concentrations were logged in all chambers over 1 h using the Multi-channel Fiber Optic Oxygen Meter Oxy-10 mini (PreSens Precision Sensing GmbH, Regensburg, Germany). Additionally, the GPP (standardized to biomass) of *Fucus* at each temperature was calculated and divided by twice the respiration rate (accounting for 12 h of photosynthesis and 24 h of respiration per day) in order to obtain the mean daily metabolic balance response of the macroalga. As response to OA (and in the KOB experiments), we only assessed NPP.

Fucus growth rate. The growth in length of *Fucus* apices (2–5 cm length) were assessed for samples exposed for 3 weeks to nine different temperatures (5–28°C, prior acclimation slope = 2.5°C d^{-1}) under a photon fluence rate of 130 μmol m^{-2} s^{-2} in a 16:8 h light:dark cycle and in a salinity of 15–16 psu (details in Supporting Information Table S1a, Graiff et al. 2015b).

Fucus reproduction rate. *Fucus* were collected in April (reproductive period) in the Wadden Sea close to the island of Sylt (Germany). Fragments with at least one immature receptacle were brought to target temperatures following a slope of 2.5°C d^{-1} and then maintained at six temperature levels between 0 and 25°C for 35 d. The percentage change in mature conceptacles over time was used as a proxy for reproductive activity (details in Supporting Information Table S1a, Graiff et al. 2017).

Fucus defenses. The effects of five levels of temperature (8, 12, 16, 21, and 23°C) on the *Fucus* defense activity against the mesograzer *I. balthica* (Weinberger et al. 2011) and common microbial (the locally common diatom taxon *Amphora*) foulers have been assessed in independent lab experiments (details in Supporting Information Table S1a, David 2009; http://oceanrep.geomar.de/7181/). The antigrazer assays were done as described above. The defenses against diatoms were assessed as for the antibacterial tests described above with the difference that the diatoms were allowed 3 h for settlement and that the plate reader assessment could be done without additional staining.

Fouling rates. Accumulation of foulers (mainly solitary and colonial diatoms) under a range of eight temperature levels (details in Supporting Information Table S1a) was assessed using eight indoor thermobaths (DC10, Thermo Scientific). Within each thermobath, two wells of a six-well plate (Sarstedt, Newtón, NC, U.S.A.) were filled with 10 mL unfiltered seawater (SW) from Kiel Fjord, and one well with 0.2 μm filtered SW served as a control. Target temperatures were obtained by gradual warming or cooling over 24 h. Photon fluence rates of 60 μmol m^{-2} s^{-1} were provided in a 12:12 h light:dark cycle using LED rows (eco+ LED-row SUNSET 3500K 33W and eco + LED-row DAY 5500K 34W, LEDAquaristik UG, Hövelhof, Germany). Daily, the well waters were replaced by fresh Fjord or filtered SW, respectively. On day 14, the established biofilm (micro- and macrofoulers) was quantitatively scraped onto a preweight filter, dried for 3 d at 60°C, and then weighed to the nearest 0.01 mg.

Grazer responses.

Grazing rates in *Gammarus* spp. Grazing rates in response to 10 temperature levels (details in Supporting Information Table S1a) were assessed in *Gammarus* spp. by quantifying the production of fecal pellets while the grazers were consuming feed pellets made of agar with embedded *Fucus* powder on a mosquito net of 1×1 mm^2 mesh (Gülzow 2015). The grazers were placed in 10 thermobaths (DC10, Thermo Scientific) containing 5–6 independent glass jars (ca. 0.25 L) with one individual of a mesograzer each. Air bubbled into each container ensured oxygenation. After 24 h, the consumed food was quantified by counting the number of emptied mesh squares. Fecal pellet production was preferred over algal biomass loss,

since the mesograzers showed sloppy feeding resulting in loss of unconsumed biomass from the feed pellet. This artifact interacted with temperature which affected the coherence of the agar (feed) pellet. As a consequence, defecation rate was found to be a more reliable metric of consumption than the (apparent) decrease in feed mass (Gülzow 2015) and, yet, related significantly to the biomass loss of the feed pellets ($r = 0.63$, $p = 0.006$).

Grazing rates in *Idotea* spp. Grazing rates in response to seven temperature levels (details in Supporting Information Table S1a) were assessed in *Idotea* spp. by quantifying the rate of fecal production, similarly to *Gammarus* spp. (see above). *Idotea* fecal pellets were collected over a period of 48 h, filtered on preweighed GF/C filter (Whatman, Germany), freeze-dried, and weighed.

Grazing rates in L. *littorea*. Grazing rates of the snail *L. littorea* were measured in response to nine temperature levels. The snails were offered preweighed pellets of artificial food based on freeze-dried *Fucus* powder (*see* Weinberger et al. 2011) and their grazing was expressed as loss weight of the pellets within 17 h. Since unlike *Gammarus* and *Idotea*, *Littorina* snails were not exhibiting sloppy feeding, the direct measure of algal weight loss could be used to assess grazing rates. Consumption was standardized as g pellet per size or weight of grazer per hour.

Responses to pCO_2

To test the responses of single species to pCO_2 levels, we selected two important players in the community: the foundation species *F. vesiculosus* and its prime grazer, *Idotea spp.* Other local species or traits of species had been shown previously to be insensitive to OA in the range (400–1100 ppm CO_2) tested in the present study: *M. edulis* (Appelhans et al. 2012), *A. rubens* (Appelhans et al. 2012), *A. improvisus* (Pansch et al. 2012), and the defenses of *F. vesiculosus* against herbivory, micro-, and macrofoulers (Raddatz et al. 2017).

Fucus photosynthetic rate. Thirty *Fucus* individuals were collected in the Kiel Fjord (54°38′N 10°20′E) and transported to the climate chamber facilities of GEOMAR. Each individual was placed in a 1-liter glass jar at ambient pCO_2 level of 400 μatm. The pCO_2 levels were gradually increased to five levels by bubbling air enriched to different levels of pCO_2: ambient (400 μatm), 900 μatm, 1400 μatm, 2400 μatm, and 3900 μatm—leading to pH levels: 8.30, 8.00, 7.90, 7.60, and 7.30—with six replicates at each pCO_2/pH level (Supporting Information Table S1a). A flow-through of sand-filtered seawater of 270 mL h^{-1} was realized. Irradiation was 93 (SE 4.6) μmol photons m^{-2} s^{-1} in a 12:12 h light: dark regime. The net photosynthetic rate (NPP) of each *Fucus* individual was measured in 2-h incubations as oxygen production using an oxygen optode (Oxi3315, WTW, Germany) and standardized to g DW obtained at the end of the experiment.

Idotea spp. feeding. Grazing rates of *Idotea* spp. in response to five pCO_2 levels (400, 900, 1400, 2400, and 3900 μatm) were measured similarly to the thermal response of these grazers (see above), that is, as the production of fecal pellets over a period of 24 h standardized to *Idotea* length (mg DW fecal pellets length^{-1}) (Supporting Information Table S1a).

Statistical analysis
KOB experiments: Effect size analysis
To compare between different response types (e.g., biomass, abundance, growth) across different taxa and functional groups, effect sizes were calculated as Hedges' g (which in contrast to log response ratios can handle zeros or negative values) (Hedges et al. 1999):

$$\text{Hedges}'\,g = \frac{\bar{x}_T - \bar{x}_c}{S_{\text{within}}} \times \left(1 - \frac{3}{4\text{df} - 1}\right) \qquad (1)$$

where $\bar{x}_T$ is the mean of the response variable in the treatment group, $\bar{x}_c$ is the mean in the control, S_{within} is the within-groups standard deviation pooled across groups, and df are the degrees of freedom used to estimate S_{within} according to the formula:

$$S_{\text{within}} = \sqrt{\frac{(n_T - 1)s_T^2 + (n_c - 1)s_c^2}{n_T - n_c + 2}} \qquad (2)$$

where n_T and n_c are sample sizes, S_T and S_c are standard deviations of the treatment and control groups, respectively. The variance of g was calculated as:

$$\hat{\sigma}^2{}_g = \left(1 - \frac{3}{4\text{df} - 1}\right)^2 \times \left(\frac{n_T + n_c}{n_T \times n_c} + \frac{\left(\frac{\bar{x}_T - \bar{x}_c}{S_{\text{within}}}\right)^2}{2(n_T + n_c)}\right) \qquad (3)$$

In the KOB experiments, the tanks with ambient temperature and pH regime were used as control, and the temperature and/or pH-manipulated tanks (OW—warming, OA—acidification, OAW—combined warming and acidification) as treatment.

KOB experiments: Meta-analysis
The R software R Development Core Team 2014 with the package metafor was used for effect size aggregation (Viechtbauer 2010) based on Hedges' g as an effect size metric. A random-effects meta-analysis model was used to calculate summary effects and confidence intervals (CI) across different responses of the same functional group (e.g., *Mytilus* and *Amphibalanus* as filter-feeders; *Littorina*, *Idotea* and *Gammarus* as grazers) to better account for heterogeneity in the data sets (Borenstein et al. 2009, 2010).

KOB experiments: Multivariate analyses
Two-way permutational multivariate analyses of variance (PERMANOVA) were performed to test for temperature and pH

effects and their interactions (crossed-design, 9999 permutation runs) on the mesocosm communities (biomass and abundances of *Fucus* system components, Euclidean distance matrices, to handle negative values). A two-way SIMPER routine was applied to test which taxa drives variability in each community and the dissimilarity between different pairs of treatments. Distance-based linear model routine (DistLM) was applied in order to analyze and model the relationships between the communities and the manipulated factors (temperature and pH). The selection criterion adopted was the Akaike information criterion (AIC), and a stepwise selection procedure was used, which optimizes selection of variables explaining most variation in the community data. Distance-based redundancy analysis (dbRDA) ordination was performed to visualize the fitted DistLM models (Legendre and Anderson 1999). All the multivariate analyses and visualizations were conducted per each seasonal KOB experiment using Primer-E V6.1.15 software package (Clarke and Gorley 2006) with PERMANOVA (Anderson et al. 2008).

Benchtop experiments: Performance modeling

To establish a TPC or a pCO_2 performance curve for each benchtop experiment, the bivariate data (temperature/pCO_2, performance response) were analyzed and fitted to quadratic, Gaussian, and exponentially modified Gaussian (EMG) models in R (package pracma, Borchers 2015) and TableCurve 2D v5.0.1 (Systat Software, 2002), following Angilletta (2006). To constrain the thermal performance models, lethal temperature values, based on former experiments or literature, were added to the data (detailed in Supporting Information Table S1). The models were compared using r^2 and corrected Akaike information criterion (AICc) using the R package bbmle (Bolker 2017). Model comparisons are detailed in Supporting Information - Table S1b. We selected the best models for each response based on optimal description of the data (r^2) and biological reasoning (i.e., no inverse quadratic fit).

Comparison of the thermal performances obtained from benchtop and KOB experiments

To allow for comparisons between the single-component (benchtop) and community experiments, we proceeded in three steps: (1) we defined the thermal comfort zones (CZ) of single species performances, (2) we projected the CZ-based "performance diamonds" of the comfort zones onto the "ambient" and "warmed" temperature regimes of the KOB experiments to allow an appreciation of how the performances of the different components of the community could be expected to change with treatment and season, and (3) we estimated the expected effect of "warming" by quantifying the degree-days (= degrees above or below the comfort zone multiplied by the number of days this condition was found) producing the metric "degree heating or cooling days."

Based on the best fitting TPC model (Supporting Information - Table S1b), we defined the critical temperatures (following Woodin et al. 2013; Sinclair et al. 2016), (Fig. 1): LT_{min} = lower lethal temperature, where an organism dies of the cold stress,

CT_{min} = minimal critical temperature where the energetic budget of an organism drops to zero in response to cold stress, the thermal comfort zone characterized by T_{low67} = cold end of the comfort zone where performance is 67% of the maximal performance, T_{opt} = optimum temperature where performance is maximal or 100%, T_{high67} = warm end of the comfort zone where performance is 67% and beyond which it drops rapidly, CT_{max} = maximal critical temperature where performance or energetic budget drop to zero, LT_{max} = upper lethal temperature where the organisms dies of heat stress. To allow a graphical assessment of the overlap between species thermal comfort zones and ambient temperatures, we overlaid "thermal performance diamonds" on the temperature regimes of the KOB experiments, using the optimal temperatures as the position of the horizontal diagonal of the rhomboid and the thermal comfort limits as the upper and lower edges of the vertical diagonal (Fig. 8).

For each season and species, we calculated how OW changed thermal stress, that is, the degree-days spent either below T_{low67} or above T_{high67}. When warming led to a decrease in the cold degree-days, it was predicted to be beneficial. When warming increased the hot degree-days, it was predicted to be detrimental. These predictions based on benchtop performance curves in combination with KOB temperatures were then correlated to the measured effects of warming on the same (or similar) responses in the community context (KOB experiments). Note, that regarding primary production we used NPP for the comparison since this was the trait measured in the KOB. Mismatches between the modeled single-species effects and the natural community-context effects hint at modulating effects of biotic interactions.

Results

KOB experiments

Fucus *performance*

Fucus *length growth* was slightly enhanced under OA, OW, and OAW in spring, strongly reduced under OW in summer, not impacted at all in autumn and favored under OA and OAW in winter (Fig. 2).

Photosynthetic activity NPP (measured as O_2 production) of *Fucus* was slightly favored under OA in spring, very strongly reduced under OW and OAW in summer, but was insensitive to OA or OW in autumn and winter.

Reproduction was reduced under OW and OAW in spring, summer and autumn, and slightly enhanced under OA in autumn and winter.

Energy storage in the form of mannitol was significantly reduced by OW in the summer and winter, and reduced by OAW in all seasons except autumn.

Fucus *defenses*

The chemical antibacterial defenses of *Fucus* were slightly weakened under OAW in autumn and under all treatments in winter (Fig. 3). The defense against the settlement of *Mytilus* larvae was weakened under OW and OAW in summer, under OA in autumn, and under OAW in winter. The defenses
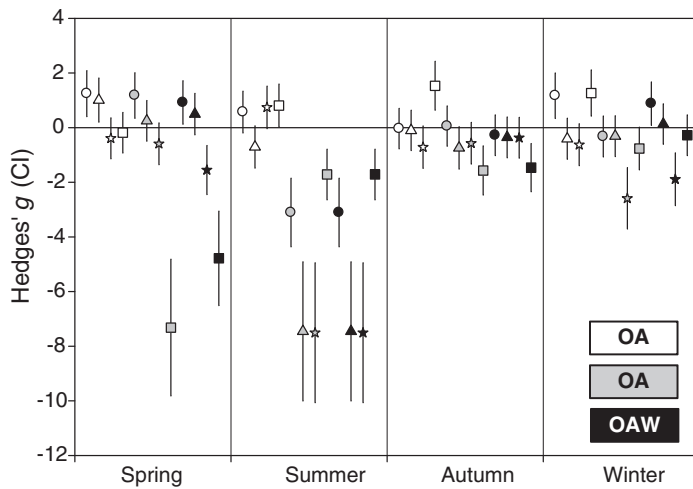
Fig. 2. *Fucus* performance. Effect sizes (Hedges' *g*) and CI of four performance traits of *F. vesiculosus* (growth: circles, photosynthesis: triangles, energy storage: stars, reproduction: squares) in response to OA (white fill), OW (gray fill), and their combination (OAW, black fill) in a community context (KOB experiments) during four seasons. Positive values signal an enhancement of the performance trait by a given treatment factor, negative values a reduction of the trait. When the CI bar does not cross the zero line, an effect is considered significantly positive or negative. When CI bars of two trait responses do not overlap, they significantly differ in strength.

against barnacle larvae settlement were enhanced under OW and OAW in spring, weakened under OAW in summer, stronger under OW in autumn, and unaffected in winter. The defenses against herbivory (with *Idotea* as proxy grazer) were strongly enhanced by OA but at the same time strongly weakened under OW and OAW in summer, in winter they were enhanced by OA and weakened by OAW. No effects on antiherbivory were observed in spring and autumn.

Fucus *epiphytes*

The biomass accrual of microepiphytes on *Fucus* was enhanced by OA, OW, and OAW in summer, and reduced by OA and OW in winter (Fig. 4). The biomass growth of macroepiphytes was enhanced by OW and OAW in spring, by OW in summer and autumn, and by OA in autumn.

Grazers

The population growth of the mesograzer *Idotea* was favored by OW and OAW in spring, autumn and winter, impeded by OW and OAW, and enhanced by OA in summer (Fig. 5). Population growth of *Gammarus* was favored by OW and OAW in autumn and winter, but strongly reduced by both treatments in summer. The population size of the grazer *Littorina* was favored under OW in autumn, but reduced by OA in spring and OAW in summer.

Filter feeders and their predator

The growth rate of the filter feeder *Mytilus* was slightly negatively impacted by OA and OAW in spring and summer, but not significantly affected by any treatment in autumn and winter (Fig. 6). The growth rate of another filter feeder, *Amphibalanus*,
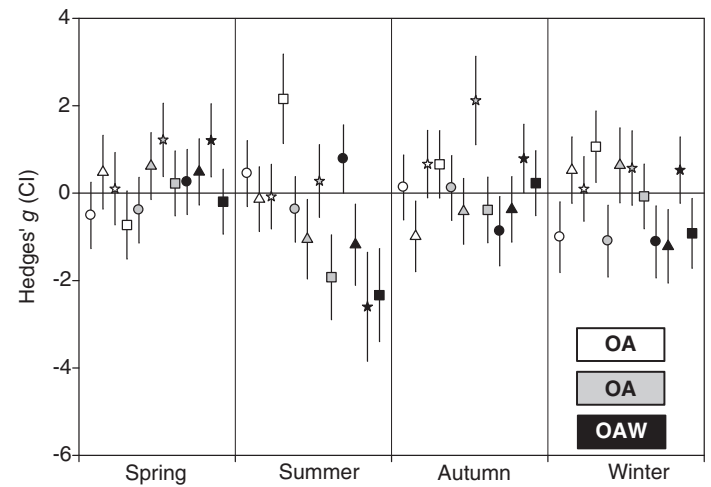

Fig. 3. *Fucus* defenses. Effect sizes (Hedges' *g*) and CI of four types of chemical defense of *F. vesiculosus* against bacterial settlement (circles), mussel settlement (triangles), barnacle settlement (stars), and grazing (squares) in response to OA (white fill), OW (gray fill), and their combination (OAW, black fill) in a community context (KOB experiments) during four seasons. Positive values signal an enhancement of the performance trait by a given treatment factor, negative values a reduction of the trait. When the CI bar does not cross the zero line, an effect is considered significantly positive or negative. When CI bars of trait responses do not overlap, they significantly differ in strength.

was enhanced by OW and OAW in summer and autumn, and enhanced by OA but reduced by OAW in winter. The survival of the sea star *A. rubens* was unaffected by all factors in spring, autumn, and winter, but strongly reduced by OW and OAW in summer.
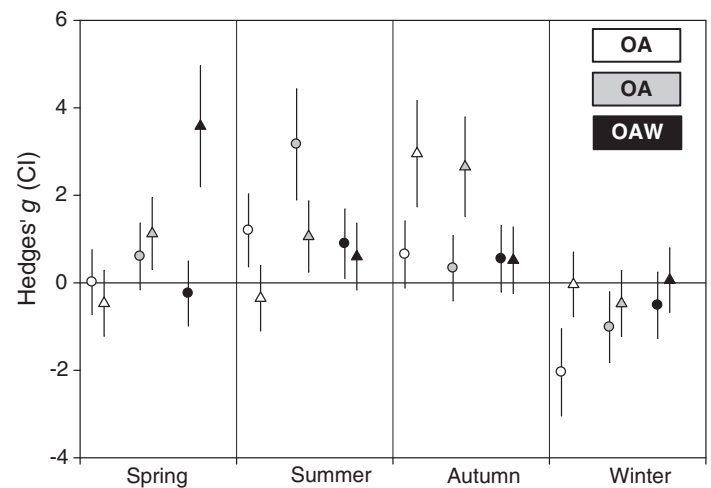

Fig. 4. *Fucus* epiphytes. Effect sizes (Hedges' *g*) and CI of the recruitment of micro- and macro-epiphytes on the thallus surface of *F. vesiculosus* in response to OA (white fill), OW (gray fill), and their combination (OAW, black fill) in a community context (KOB experiments) during four seasons are shown. Positive values signal an enhancement of the performance trait by a given treatment factor, negative values a reduction of the trait. When the CI bar does not cross the zero line, an effect is considered significantly positive or negative. When CI bars of trait responses do not overlap, they significantly differ in strength.
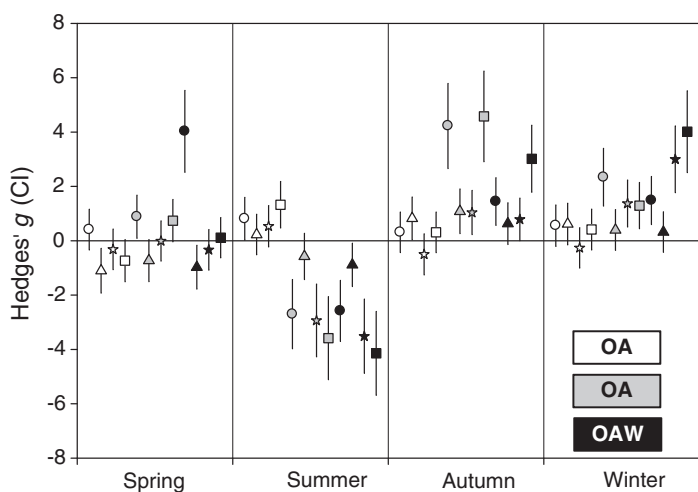
Fig. 5. Mesograzer populations. Effect sizes (Hedges' *g*) and CI of the population sizes of main mesograzer taxa *Idotea* sp. (circles), *L. littorea* (triangles), *Gammarus* sp. (stars), and their combination (squares) in response to OA (white fill), OW (gray fill), and their combination (OAW, black fill) in a community context (KOB experiments) during four seasons. Positive values signal an enhancement of the performance trait by a given treatment factor, negative values a reduction of the trait. When the CI bar does not cross the zero line, an effect is considered significantly positive or negative. When CI bars of trait responses do not overlap, they significantly differ in strength.

Community restructuring

The two-way PERMANOVA for temperature and pCO_2 effects on the communities was significant for temperature in all
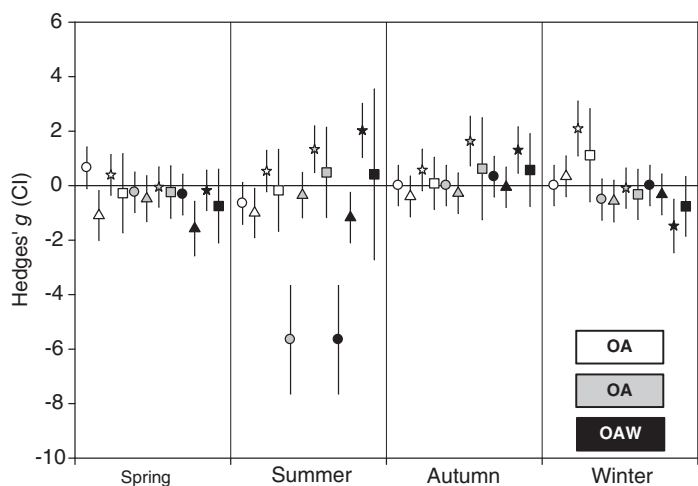
Fig. 6. Filter feeders and predators. Effect sizes (Hedges' *g*) and CI survival of the predatory seastar *A. rubens* (circles) and of the individual growth rates in the filter feeding mussel *M. edulis* (triangles), the barnacle *A. improvisus* (stars), and their combined response (squares) to OA (white fill), OW (gray fill), and their combination (OAW, black fill) in a community context (KOB experiments) during four seasons. Positive values signal an enhancement of the trait by a given treatment factor, negative values a reduction of the trait. When the CI bar does not cross the zero line, an effect is considered significantly positive or negative. When CI bars of trait responses do not overlap, they significantly differ in strength.

seasons but spring, while pCO_2 was not significant at any point in time (Fig. 7A–D, Supporting Information Tables S2–S13).

The interaction between temperature and pCO_2 was not significant in any season. The two-way SIMPER analyses revealed that in spring, the biomass increase of *Fucus* and of the grazer *Idotea* in the warmed treatments cumulatively explained 34% of the dissimilarity between communities (Supporting Information Table S6). In summer, the decrease in the survival of the predator *Asterias* and in the abundances of the grazer *Idotea* had the greatest cumulative contribution to the dissimilarity between the temperature treatments (41%) whereas the increase in growth of *Mytilus* and *Fucus* under OA had the greatest cumulative contribution (48%) to the marginally significant ($p = 0.057$) dissimilarity between the pCO_2 treatments (Supporting Information Table S7). In autumn, the increase in survival, growth, and abundance of all the species in the community except *Mytilus* under warming contributed similarly (10–18% each) to the dissimilarity between the temperature treatments (Supporting Information Table S8). In winter, the increase in the abundance of the grazers *Idotea* and *Gammarus* under warming had the greatest cumulative contribution (44%) to the dissimilarity between the temperature treatments (Supporting Information Table S9). dbRDA biplots explained more than 50% of the total variance of the communities in all seasons, and more than 60% in the summer and winter (Fig. 7A–D). The DistLM results indicated, again, that temperature was the only factor significantly affecting the structure of the communities in all seasons (Supporting Information Tables S10–S13).

Benchtop single-component experiments

The parameters of the TPCs, the goodness-of-fit (r^2), and corrected AICc for the quadratic, Gaussian, and EMG models are detailed in Supporting Information Table S1.

In response to PAR, *Fucus* P_{max} was about 28 nmol of O_2 cm^{-2} s^{-1} and *Fucus* reached 50% saturation at a photon flux of ca. 42 μmol m^{-2} s^{-1} (Supporting Information Fig. S1a). Thus, for the range of irradiation levels used in the various experiments (93–165 μmol photon m^{-2} s^{-1}), *Fucus* performance in terms of oxygen production was between 71% and 82% of P_{max}.

Thermal responses

Fucus *responses.*

Fucus metabolic balance. The ratio of GPP to respiration (both in mgO$_2$ L^{-1} h^{-1} g^{-1} (WW of Fv)) Wet Weight of *Fucus vesiculosus* showed a quadratic response to temperature (Supporting Information Fig. S1b, $R^2 = 0.71$) with an optimum (2.5-fold more daily O$_2$ production than consumption) around 10°C. a comfort zone between −1°C and 21.4°C and transition into heterotrophic metabolism (GPP/2R < 1) around 26°C.

Fucus growth. Relative growth rates of *Fucus*, assessed as relative change in tip length (Graiff et al. 2015*b*), approximately doubled when temperature increased from 5 to 15°C, reached a
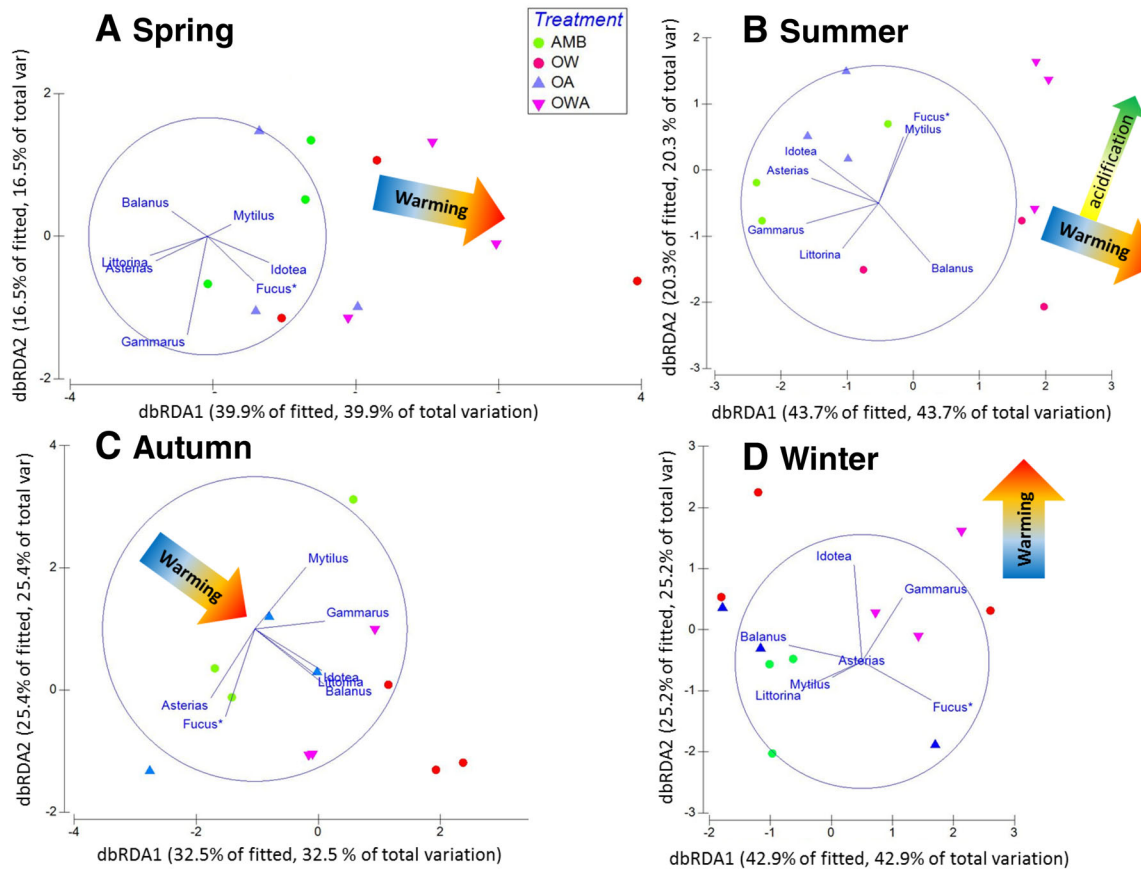
Fig. 7. Community shifts (as two-dimensional dbRDA plot) under the influence of warming (blue-red arrow) and acidification (green-yellow arrow) in (**A**) spring, (**B**) summer, (**C**) autumn, and (**D**) winter. OA only contributes (weakly) to the summer restructuring, but is without any effects in spring, autumn, or winter. Dots represent the communities under ambient pCO$_2$ level, triangles the communities under acidified conditions. Blue or green are the communities under ambient temperature whereas pink or red symbols are the communities under warmed conditions. The overlain vectors indicate in which sense and to which extent selected species contributed to the dissimilarities of the communities in response to warming (and summerly acidification). As an example, in summer, *Fucus* and *Mytilus* benefitted from acidification, *Asterias* and *Idotea* suffered from warming.

peak of about 2.8% d^{-1} at 15°C, then rapidly decreased to zero between 26 and 28°C (Supporting Information Fig. S2). The comfort zone for this response ranged between 7.7 and 22.4°C. The best fitting model was quadratic ($r^2 = 0.9$).

Fucus reproduction. In the lab, the maturation of *F. vesiculosus* showed a clear temperature dependency (Gaussian, $r^2 = 0.67$) with highest prevalence of fertile conceptacles around 9°C (Supporting Information Fig. S3, Graiff et al. 2017). The comfort zone for *Fucus* reproduction ranged from 3.8 to 14.7°C.

Fucus defenses. Antifouling defenses

The chemical defenses of *Fucus* against diatoms were strongest around 15.5°C and exhibited a comfort zone between 8 and 23°C (quadratic fit, $r^2 = 0.8$) (Supporting Information Fig. S4).

Antigrazing defenses

Temperature affected the capacity of *Fucus* to induce chemical antifeeding defenses in response to grazing as shown by Weinberger et al. 2011 (Supporting Information Fig. S5). Strongest defenses were observed at 18°C, and the defense comfort zone ranged from 14.1 to 21.8°C (Gaussian fit, $r^2 = 0.6$).

Fouling pressures. Accumulation of micro- and macro-fouling algae on artificial substrata exposed to natural unfiltered SW showed a quadratic relationship ($r^2 = 0.6$) with temperatures from 5 to 35°C. Fouling rate peaked at 18.5°C and exhibited a wide comfort zone between 6.8 and 30.2°C (Supporting Information Fig. S6).

Grazing rates. All grazers showed a monomodal relation between grazing rates and temperature albeit with a relatively large scatter (r^2 between 0.42 and 0.68). *Littorina* grazing rates peaked at 17.3°C (Supporting Information Fig. S7) and showed

a comfort zone ranging from 5.2 to 22.5°C (EMG fit, $r^2 = 0.52$). *Idotea* defecation rates (as a proxy for consumption) showed a maximum around 13.6°C with a comfort zone between 4.8 and 22.5°C (quadratic fit, $r^2 = 0.6$, Supporting Information Fig. S8). The defecation rates of *Gammarus* spp. (as a proxy for consumption) followed temperature (EMG $r^2 = 0.41$, Supporting Information Fig. S9) and showed a maximum at 20.6°C with a comfort zone ranging from 14.8 to 24.1°C.

Responses to pCO_2

Fucus *photosynthetic rates.*   The NPP of *Fucus* showed high variability with no correlation to pCO_2/pH levels (quadratic fit, $r^2 = 0.09$, Supporting Information Fig. S10).

Idotea *grazing rates.*   The grazing rates of *Idotea* showed high variability with no correlation to pCO_2/pH levels (quadratic fit, $r^2 = 0.07$, Supporting Information Fig. S11).

Expected changes of specific performances in a fluctuating temperature regime

Sorted from colder to warmer T_{opt}, the sequence of the respective species-specific responses was: *Fucus* reproduction, *Fucus* metabolic balance, *Idotea* grazing, *Fucus* growth, *Fucus* antifouling defenses, feeding pressure by *Littorina*, *Fucus* antigrazing defenses, fouling pressure, and *Gammarus* grazing pressure (Fig. 8, Supporting Information Table S1b).

The width of the thermal range over which the various performances were larger than 67% of optimum also varied substantially. Indeed the width of the comfort zones increased from *Fucus* antigrazing defense over *Gammarus* feeding to *Fucus* reproduction and growth, *Fucus* antifouling defense, *Littorina* and *Idotea* feeding, *Fucus* metabolic balance and, finally, to fouling pressure. Under OW, the warm stress zone (extending beyond the upper comfort boundary) was sequentially reached by *Fucus* reproduction then—almost simultaneously—by *Fucus* metabolic balance, growth, defenses, by grazing and finally by fouling pressure. The most obvious mismatch is found in the functional "pair" fouling and antifouling where the defense passes its maximum 4° (or ca. 4 weeks with regard to seasonal in situ temperature) before fouling and reaches the warm stress zone 7° before the fouling pressure does.

If there were no other factors besides temperature—such as nutrient and light fluctuations, or biotic interactions—affecting these responses, we would expect the following seasonal phenology (Fig. 8): Early in spring (April, 5–10°C), *Fucus* performance increases, then from 10°C upward (early May) grazing intensifies first by *Littorina* and *Idotea*. Slightly later, fouling rates and antifouling defenses intensify, followed by an increase in grazing by *Gammarus* and in antigrazing activity of *Fucus* above 14°C (mid-June). On the warm side of the comfort zones, *Fucus* performance decreases beyond 15–18°C, followed by a decline in cumulative grazing by the three taxa
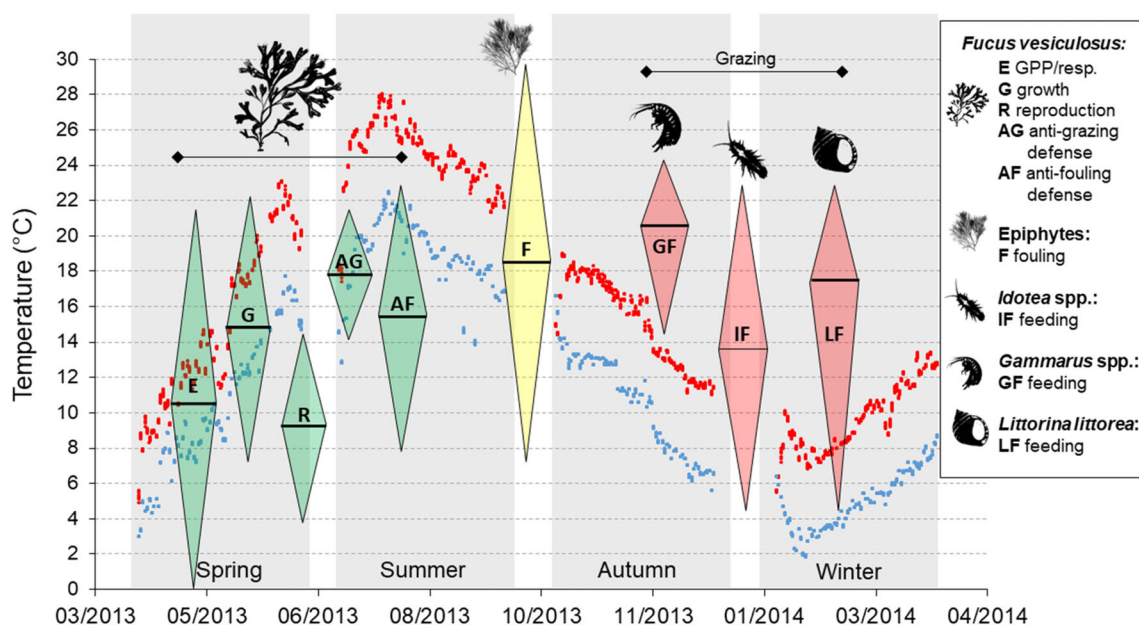
Fig. 8. Projection of the performance diamonds onto the ambient (blue dots) and warmed (red dots) temperature regimes in the four seasonal KOB experiments (gray fields). Since both the ranges of the comfort zones (vertical axis of the diamond) and the position of optimal temperatures (short axis of the diamond and horizontal lines) differ among response traits, at any given temperature the traits will be at different distances from their optimum. As a consequence, interactions will shift as temperature changes with season or with (simulated) OW. As an example, antigrazing defenses of *F. vesiculosus* are strongest at around 18°C but will have substantially weakened when temperatures approach 22°C where fouling pressure is still substantial. The inset table gives the modeled optimal temperature and comfort zone boundaries for the various responses. AF, *Fucus* antifouling defense; AG, *Fucus* antigrazer defense; E, *Fucus* metabolic balance GPP/respiration; F, fouling pressure; G, *Fucus* growth rate; GF, *Gammarus* defecation; IF, *Idotea* defecation; LF, *Littorina* grazing rate; R = *Fucus* reproduction.

beyond 19°C. Fouling shows the widest comfort zone extending to 30°C.

Discussion

Our approach, to combine single-species benchtop experiments and integrated system-based KOB experiments using the same experimental community components, revealed that (1) OW is a much stronger driver than OA (in the examined Baltic Sea system), (2) the divergent thermal comfort zones of interacting species indicate the potential for interaction shifts, (3) the potential of biotic interactions to modulate direct OW impact varies with season, and (4) extrapolating thermal responses from benchtop to community level may be valid when the thermal stress is strong (very cold or very warm) but less so when it is moderate (Table 1).

The direction and strength of the effects of warming and acidification on species in a Baltic Sea shallow benthic community varied substantially among drivers, components (species or functional groups), responses, and seasons. A stronger impact of OW as compared to OA has been reported before for various marine organisms (e.g., Eklof et al. 2015) and is not surprising since the quasi totality of ectothermic organisms (animals and plants) show a ubiquitous direct and strong physiological response to temperature (Dell et al. 2014) while acidification may impact only specific functional groups (Sommer et al. 2007; Paul et al. 2015). Similarly, in our benchtop experiments, pCO_2 level explained less than 10% of variation in the response of *Fucus* and its main grazer. Since these findings correspond well with the results of KOB experiments and previously published results (Appelhans et al. 2012; Pansch et al. 2012; Raddatz et al. 2017), we concentrated our analyses and predictions on OW as the dominant driver.

In the community context, OW impacted *Fucus* performance traits relatively little in spring, autumn and winter with the exception of an OW driven decrease of reproduction and energy storage. These two traits as well as growth were particularly strongly reduced by summer warming. OA, in contrast, was mainly beneficial to *Fucus* performance in all seasons. *Fucus* defenses against foulers and consumers were moderately (winter) to strongly (summer) reduced by OW, but much less impacted in spring and autumn. *Fucus* epiphytes, by contrast, benefitted from OA and OW in all seasons except winter. The population level biomass of grazers (reflecting reproduction and/or individual size) was enhanced by OW in autumn and winter, but strongly decreases in summer. Sessile filter feeders, potential space competitors of *Fucus*, were generally weakly or not affected by OA or OW except in summer when sea star survival was severely jeopardized by OW. In all seasons except spring, OW tends to shift the community structure in favor of heterotrophs.

How much of these compound effects—which were a result of the single or combined influence of treatment factors OA, OW, and OAW plus the other uncontrolled and seasonally variable environmental factors plus biotic interactions—could have been predicted from the organism-level performance curves established in the lab? The projection of the performance diamonds onto the temperature regime in the four seasonal KOB experiments (Fig. 8) suggests the following: whenever the ambient temperature is more than 5°C lower than T_{opt} or even lower than T_{low67} (with regard to a specific response), the simulated OW should be beneficial. If the ambient temperature is close to or above T_{opt}, warming would be detrimental. Broadly, *Fucus* traits tend to be more cool-adapted while grazers and filamentous algae are more thermophilic. Thus, in the cold months, warming should be beneficial to all system components, but with increasing water temperatures towards the summer, a sequential decline in (1) some *Fucus* fitness traits (reproduction, growth, metabolic balance), (2) cumulated feeding pressure (isopods, amphipods, gastropods) and *Fucus* defenses (antigrazing, antifouling) and, finally, (3) fouling pressure would be triggered by OW. Interestingly, while NPP increases with warming up to 26°C, growth and reproduction do not follow. This may be indicative of excess energy obtaining under rising temperatures being rather used for stress compensation (e.g., Thomsen et al. 2013; Pansch et al. 2014) than invested into growth or reproduction. In consequence, *Fucus* would be most impacted by OW in summer when its performance is heat-stressed, its defenses are weakened and the biotic pressures by grazing (especially by amphipods, Werner and Matthiessen 2013; Werner et al. 2016*b*) and by fouling respond less sensitively to warming until first grazers then foulers, too, succumb to the highest temperatures. In contrast, at suboptimal temperatures in winter most processes and species assessed in this study should respond positively to warming. These theoretical expectations match the observed community-level responses to OW qualitatively well in summer (mostly negative) and, to a lower extent, in winter (neutral to positive) (Table 1) but less so in autumn and spring (generally more beneficial than expected). In fact, OW impact as predicted by the TPC models and as experienced in the KOB experiments relate well for the pooled summer-winter effects (Spearman Rank Correlation $r = 0.63$, $p = 0.005$, $N = 18$) but not for the pooled spring-autumn effects ($r = 0.054$, $p = 0.82$, $N = 18$). Due to the shape of the performance curves with shallowest slopes at intermediate temperatures, any degree of warming in the coldest and hottest season should impact performance strongest. The main mismatches are that, in the compound (KOB) responses, there are fewer positive effects of warming on *Fucus* in winter, and more positive warming effects on grazers and foulers (except in winter) than expected from the TPCs. The absence of those beneficial warming effects on *Fucus* performance and defenses in winter, as could be inferred from the interaction-free TPC, may be attributable to a lack of energy, which cannot be acquired in the (dark) winter months. Additionally, in winter any enhanced primary production may have been counteracted by OW-enhanced grazing on young and photosynthetically most active thallus parts (Jormalainen et al.

2001*b*) (Fig. 4). It may seem surprising that antigrazer defenses were not upregulated as grazing pressure increases with warming in these seasons (Rohde and Wahl 2008). However, the production of these defense metabolites in *Fucus* is thought to drain its energy reserves (Hemmi et al. 2004) which might still have been available in the (short) benchtop experiments, but not to the same extent under conditions of reduced underwater light in spring, autumn, and winter (Lehvo et al. 2001) in the KOB. Additionally, OW reduces mannitol content in all seasons (Graiff et al. 2015*a*). According to the metabolic theory of ecology (Brown et al. 2004), metabolic (including grazing) rates should ultimately affect population size. It is therefore not surprising that both traits, at least for the crustacean grazers, simultaneously increased with warming to a peak between 15 and 20°C and strongly declined beyond 24°C. *Littorina* grazing peaked at lower temperatures whereas its population dynamics could not be properly assessed since these snails hardly reproduced in the tanks. Typically, mesograzers are omnivores exhibiting feeding preferences (Wahl and Hay 1995; Jormalainen et al. 2001*a*; Jaschinski et al. 2011). Their feeding choice behavior and, thus, the fate of potential prey are influenced by the prey species available (Wahl and Hay 1995; Jormalainen et al. 2008), their food quality (Hemmi and Jormalainen 2002), inducible antiherbivore defenses (Hemmi et al. 2004; Rohde et al. 2004; Rohde and Wahl 2008), and by the identity of other consumers in the system (Yun et al. 2010). All of these interactions are to some extent affected by temperature—and other global change factors such as salinity and nutrients—via shifting species distributions or phenologies (Ayres 1993), temperature sensitivity of defenses, or concentration of energy reserves affecting food quality (Korpinen et al. 2007; Weinberger et al. 2011; Rothausler et al. 2017). This complexity may explain why the warming effects extrapolated from interaction-free benchtop experiments differ somewhat from those found in the community context—except in summer and winter when warming enhanced thermal warm stress or decreased thermal cold stress, respectively.

Epibiosis (fouling) is another potential biotic pressure on *Fucus* (i.e., the number of organisms settling and growing per unit time and surface), responding negatively to antifouling defenses of the host and grazing pressure by mesograzers. Fouling pressure increases with water temperature (Wahl et al. 2010; Werner and Matthiessen 2017) up to a threshold where thermal stress begins to reduce micro- and macroalgal foulers as was found in our study. The epibiotic community is mainly composed of numerous bacterial strains, various sessile protozoans, diatoms (both solitary and colonial), and filamentous algae (e.g., Jormalainen et al. 2008; Lachnit et al. 2009; Werner and Matthiessen 2013). While it is not surprising that warming is beneficial to the epiphytes in spring and autumn, the unexpected enhancement of fouler biomass in summer when the foulers' T_{opt} is exceeded and (slight) reduction in winter in the warmed treatments may be an indirect outcome, reflecting the OW-driven reduction in summer and increase in winter of

grazer populations. However, not only grazer population size is affected by warming, but also the per capita grazing rates. Interaction-free TPCs suggest that the cumulative consumption rates of the three most important grazer taxa are negatively impacted by warming in summer but enhanced in the other seasons. The modeled predictions regarding per capita feeding, thus largely match the community level responses of population dynamics, which ultimately depend on individual energy intake, growth, and reproduction. In consequence, the stronger-than-expected epiphyte biomass in spring and autumn under OW despite simultaneous enhancement of grazing could be attributable to favorable nutrient and light conditions in these seasons, while the high fouling in summer despite low nutrient levels is certainly due to the breaking down of grazing control under warmed conditions (smaller populations and lower grazing rates). For the host macrophyte, OW-enhanced epiphytism reduces light availability at the thallus surface (Wahl et al. 2010) and nutrient availability (Korpinen et al. 2007). The latter effect may be particularly strong in (early) summer when nutrients are low and OW reduces grazing control.

Our approach, testing and comparing the response of organisms individually and in the community context, strongly suggests that ignoring (1) seasonal variability and (2) the modulating effect of biotic interactions which buffer or enhance the direct effects of OW in situ (and other global change factors), may lead to off-target perceptions (e.g., Doney et al. 2012; Russell et al. 2012; Harley et al. 2017; Wahl et al. 2018). However, these extrapolations from benchtop TPCs to KOB responses excluded, among other factors, the modulating yet weak effect of OA. When the mean effect of OA, OW, and OAW on the overall performance of *Fucus* (photosynthesis, energy storage, reproduction, growth) in the community context is considered, it becomes apparent that OA tends to be either neutral or beneficial in all seasons, possibly indicating a fertilization effect of CO_2 enrichment (Connell and Russell 2010). While the carbon concentration mechanism (CCM) in *Fucus* allows the use of the large bicarbonate pool in seawater (Johnston and Raven 1990; Gutow et al. 2014), additional CO_2 could still be beneficial by saving enzymatic energy (Young and Gobler 2016). Further limitations of this study should be considered. (1) We chose to restart the experiments between seasons in order to assess seasonal differences in climate change impacts. This entails the drawback that interseasonal carry-over effects were excluded. Thus, warming-enhanced energy depletion in *Fucus* particularly during summer could exacerbate the warming impacts in autumn. Similarly, the enhanced growth of grazer populations in autumn could lead to an even more pronounced increase in grazer numbers in winter than observed. In contrast, the warming-driven dieback of grazers in summer should limit the intensification of grazing in a warmer autumn. (2) The tanks were too small to include any viable fish populations. In the field, their presence might control to some extent the warming-driven growth of grazer populations in cooler

seasons—and thus promoted the proliferation of epiphytes (Reusch et al. 2018 and references therein). (3) Warming and acidification are not the only environmental parameters shifting under global change (BACC Author Team 2010; IPCC 2013). In particular, at the regional scale, additional anthropogenic changes may interact with, and often amplify, the global drivers OA and OW. Thus, desalination, as expected for the Baltic Sea (Meier 2006), increases osmotic stress on all organisms of marine origin and, thus, increases their susceptibility to other pressures (Rugiu et al. 2018). Nutrient enrichment favors epiphytism (Korpinen et al. 2010; Werner et al. 2016*a*) with mainly detrimental effects on host algae (Wahl et al. 2011, 2015*b*), reduces recruitment of *Fucus* (Korpinen and Jormalainen 2008), and increases its consumption by mesograzers (Hemmi and Jormalainen 2002). In addition, overfishing may affect the top-down control on foulers via a trophic cascade (e.g., Korpinen et al. 2007; Reusch et al. 2018). Fouling, sedimentation, and hypoxia reduce the survival of *Fucus* offspring (Wahl et al. 2011). The sensitivities to all these drivers not only vary among species but also among genotypes (Al-Janabi et al. 2016*a*) constituting the basis for potential adaptation to a shifting world which may be favored by fluctuations of the drivers (Rilov et al. 2019). However, the low genetic diversity of the brackish *Fucus* population in the Baltic (Johannesson and Andre 2006), just as in thermal trailing edge populations in southern Europe (Pearson et al. 2009), may reduce adaptive potential.

Despite the mentioned limitations of our experiments, we may, nonetheless, dare speculating on the fate of *Fucus* communities in a warmer, more acidic, less saline, overfished, nutrient-rich, and sporadically deoxygenized Baltic Sea. *Fucus* will directly suffer from warming in summer, from desalination year-round but most intensively during summerly stratification, and from hypoxic upwelling in late summer and autumn (e.g., Al-Janabi et al. 2016*b*). At the same time, it may benefit less from acidification (having CCM) or from nutrient enrichment than its epiphytes because it can accumulate storage products in replete periods (Kawamitsu and Boyer 1999; Lehvo et al. 2001; Hemmi et al. 2005). In contrast, both factors (plus warming) may indirectly affect *Fucus* by benefitting its fast-growing competitors (filamentous benthic algae, epiphytes, phytoplankton) (Provost et al. 2017; Takolander et al. 2017). Depending on the temporal occurrence of these drivers, they may amplify or buffer each other's impact (Gunderson et al. 2016; Rugiu et al. 2018). The distributional range of Baltic *Fucus* may not move pole wards in response to the prominent driver, warming, because toward the NE Baltic osmotic stress increases along the salinity gradient (Nygard and Dring 2008). *Fucus* may neither escape the particularly stressful shallow waters by shifting its depth distribution downward because of light limitation caused by dense plankton in the nutrient rich Baltic (Torn et al. 2006). If the rate of adaptation—because of *Fucus*' low genetic diversity and long generation time—is substantially slower than climate velocity (Brito-Morales et al. 2018) in this rapidly changing environment (Reusch et al. 2018), the distributional range of *Fucus* may dramatically shrink causing functional loss to the ecosystem (Takolander et al. 2017). An alleviation of local or regional pressures such as overfishing or nutrient enrichment might reduce the pending retreat of *Fucus* as could ecoengineering measures like nutrient extraction via large-scale macroalgal cultures (Liu et al. 2010). On the other hand, the pressure on *Fucus* may be further enhanced by invasive competitors such as *Agarophyton vermiculophylla* (Hammann et al. 2013). However, *Agarophyton* may also mitigate the functional loss to the system associated with a possible decline of *Fucus* since this neobiota is functionally similar (except for its biomass reduction in winter) to *Fucus*. Furthermore, *Agarophyton* is more robust with regard to several of the global change pressures (Weinberger et al. 2008, 2013; Hammann et al. 2016) and directly benefits from OA and CO_2-rich upwelling (Young and Gobler 2016).

Concluding, the initial question whether the more laborious, longer, and more expensive mesocosm experiments are worth the extra effort can be answered affirmatively. Particularly when the environmental pressures are of moderate intensity, community-level mesocosm experiments reveal the modulating role of biotic interactions in the response of species and communities to the predicted global change.

Data availability statement

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Conflict of Interest

None declared.